

HYPERTROPHY OF MALE GENITALIA IN SOUTH AMERICAN AND AUSTRALIAN TRIAENONYCHIDAE (ARACHNIDA: OPILIONES: LANIATORES)

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Hypertrophy of male genitalic elements, particularly the stylus, is described and discussed. A stylus is regarded as hypertrophied if stylus length is sub-equal to or longer than truncus length. Greatest hypertrophy occurs in the Australian species *Cluniella distincta* Forster (stylus $\times 4.5$ truncus) and a new genus, new species from South America ($\times 2.5$ truncus). Other species discussed are *Araucanobunus juberthiei* Muñoz-Cuevas from South America, and *C. minuta* Forster, *Rhynchobunus arrogans* Hickman, *Tasmanobunus parvus* Hickman, *Tasmanonuncia* sp., *Allobunus distinctus* Hickman and *Thelbunus mirabilis* Hickman from Australia. To accommodate an elongate stylus, the truncus is often shortened, and the genital operculum and sternum modified so that the genital orifice is located more anteriorly. Hypertrophy of the stylus may be associated with the hypertrophy or reduction of other terminal elements. In *Cluniella* spp. and the two South American species penetration of the stylus occurs along a very long vagina; the spermathecae are situated at the base of the ovipositor. Hypertrophy may have evolved as a consequence of sexual selection. □ *Opiliones, Triaenonychidae, male genitalia, hypertrophy, morphology, sexual selection.*

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The triaenonychid penis comprises a basal truncus supporting an apical complex which includes the stylus and associated plates, processes and setae. In the primitive condition, three sets of plates are present (Fig. 1A): the dorsolateral plates which are embryologically derived from the truncus and the dorsal plate and ventral plate embryologically related to the stylus (Martens, 1986). Both the dorsal and ventral plates were apparently primitively paired but are now fused, at least basally. The ventral plate carries setae. Certain taxa have undergone loss or reduction of plates (Martens, 1986; Hunt and Hickman, 1993). A few taxa have undergone extreme hypertrophy in the length of the stylus with one or more of the associated plates frequently showing correlated hypertrophy, or reduction, depending on the taxon.

HYPERTROPHIED STRUCTURES

CLUNIELLA spp.

The most extreme hypertrophy of the stylus known for the family occurs in *Cluniella distincta* Forster, 1955 of SE Queensland and NE New South Wales (Fig. 2A). The stylus is $\times 4.5$ truncus length. There is correlated morphological change in the female where spermathecae occur basally

in the ovipositor (Fig. 5C), unlike the usual condition where the spermathecae occur sub-apically. Therefore, the long stylus probably penetrates almost the whole length of the ovipositor to reach the spermathecae. The dorsolateral plates of the penis are elongate, gradually tapering to $\times 2$ ventral plate length (Fig. 2B). The dorsal plate is either lacking or intimately fused with the stylus; the latter is suggested by the subterminal lateral processes on the stylus which may be homologous to terminations of the dorsal plate (see *Thelbunus mirabilis* below, Fig. 5A). The ventral plate is reduced in size, and the number of inferior setae is reduced from three to two pairs.

The extreme stylus is accommodated within the body by shortening of the truncus, and by elongation of the genital operculum and posterior invagination of the sternum which together shift the genital opening anteriorly. The sternum margins tend to follow the genital operculum (Fig. 5E; cf. female genitosternal region, Fig. 5F) but when the operculum is lifted the shape resembles that in Fig. 5H.

Cluniella minuta Forster, 1955, which overlaps in distribution with *C. distincta*, has undergone less radical elongation of the stylus (Figs 2C-D). Nevertheless, the stylus is $\times 1.4$ truncus length. The spermathecae are also basal despite the

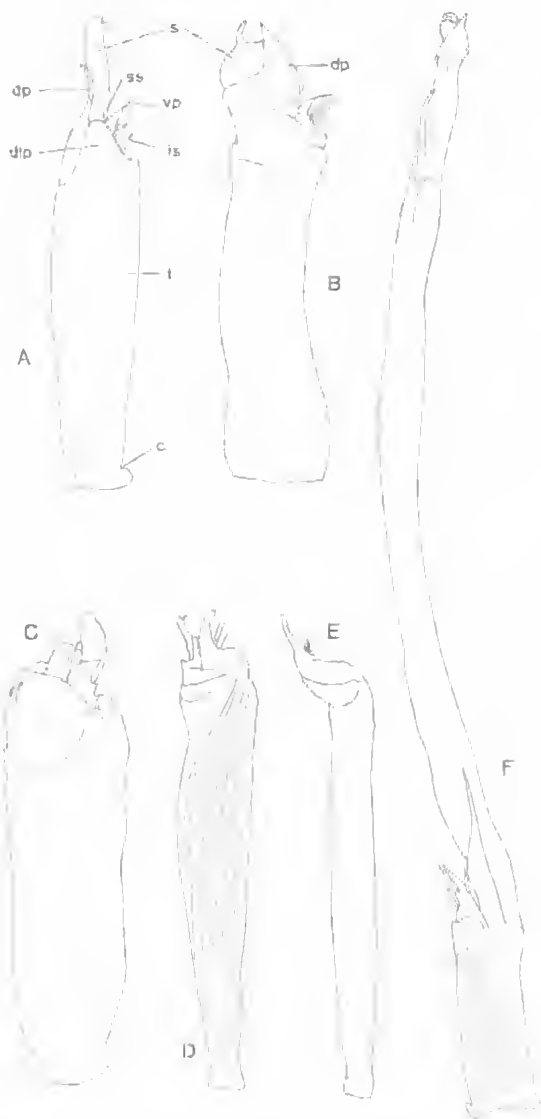


FIG. 1. Variation in δ genitalia of some Australian Triaenonychidae. A: *Hickmanoxyonoma cavaticum*; B: *Glyptobunus signatus*; C: *Tasmanonyx montanus*; D: *Dipristes serripus* (muscle shown); E: *Lomanella raniceps*; F: *Chuniella distincta* (muscle shown); c = constriction for membrane attachment; dlp = dorsolateral plate; dp = dorsal plate; is = inferior seta; s = superior seta; ss = superior seta; t = truncus; vp = ventral plate.

shorter stylus. The dorsolateral plates are elongated to a similar extent to *C. distincta* while the ventral plate, though reduced, bears 3 pairs of inferior setae. The truncus is less shortened, the genital operculum is not elongate and the sternum is long and narrow. In both species, the constric-

tion in the truncus where penis sheath membranes attach is basal.

The differences between the two species are not due to infraspecific variation, such as male dimorphism reported in some Australian genera (Hunt, 1985). Characters distinguishing *C. minuta* include a very long calcaneus compared with astragalus in leg I.

ARAUCANOBUNUS JUBERTHIEI MUÑOZ-CUEVAS, AND NEW GENUS, NEW SPECIES (MAURY, IN PREP.)

A. juberthiei from southern South America shows moderate hypertrophy of the stylus with stylus length about 1.3 truncus length (Figs 3A-B). An undescribed species referable to a new genus (Maury, in prep.), but apparently with close genitalic affinities to *A. juberthiei*, has undergone greater hypertrophy with stylus length $\times 2.5$ truncus length (Fig. 3C). The dorsolateral plates are present in both species, but the dorsal plate is apparently lost (or intimately united with the stylus). The truncus in the undescribed species is greatly shortened, in *A. juberthiei* much less so.

Both species have an elongate genital operculum and a short, subtriangular sternum (for example, see Figs 5G-I). When closed, the genital operculum virtually obliterates the sternum.

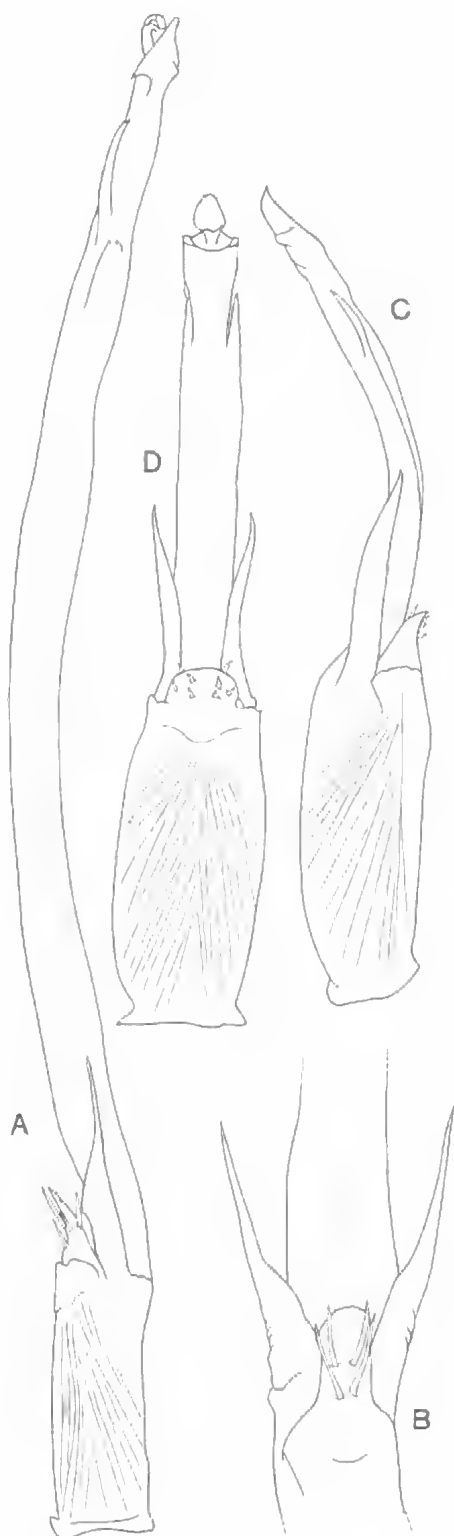
Unlike the condition in *Chuniella*, the constriction is situated mid-way along the truncus in both species (Figs 3A-D). As in *Chuniella*, the spermathecae are situated at the base of the ovipositor at the end of a long vagina (Fig. 5D: *A. juberthiei*). There appear to be no significant infraspecific variations in size or shape of the genitalia in these species.

RHYNCHOBUNUS ARROGANS HICKMAN

This species, from NE Tasmania, also has a prominent constriction at about mid-way along the truncus (Fig. 4A). *R. arrogans* belongs to a lineage distinguished by loss of the dorsolateral plates. The dorsal plate envelopes the stylus basally and terminates ventral to it. *R. arrogans* is very close to, if not congeneric with, *Glyptobunus signatus* Roewer (Hunt, in prep.). The stylus is $\times 1.3$ truncus length. The spermathecae are subterminal. The ventral plate is reduced but still carries the normal complement of setae for this lineage (Figs 4A-B). *R. arrogans* has an elongate genital operculum but lacks a triangular sternum.

TASMANOBUNUS PARVUS HICKMAN

This species is closely allied to, or possibly congeneric with, *R. arrogans* and *G. signatus* as



it lacks dorsolateral plates, its stylus carries a subdistal dorsal barb, and the dorsal plate terminates ventral to the stylus (Figs 4C-D). The stylus is subequal in length to the truncus and the dorsal plate has undergone complementary elongation. The constriction around the truncus is more subdued and situated somewhat more basally.

TASMANONUNCIA N.SP.

This species belongs to the same general lineage as *R. arrogans* in that it lacks dorsolateral plates (Hunt, in prep.). However, the stylus carries a subdistal dorsal tuft of hairs instead of a single barb (Figs 4E-F). Stylus length is subequal to truncus length and, as with *Tasmanobunus parvus*, the dorsal plate is greatly elongate.

ALLOBUNUS DISTINCTUS HICKMAN

A. distinctus, from NW Tasmania, has a prominent constriction mid-way along the truncus. The stylus is modestly elongate, being subequal in length to the truncus. The ventral plate, however, is hypertrophied, uniting with other sclerotisations to form an elongate cylinder around the proximal half of the stylus (Figs 4G-H). The male of *A. distinctus* has a triangular sternum and a moderately elongate genital operculum.

THELBUNUS MIRABILIS HICKMAN

Unlike the *Rhynchobunus* lineage, this NE Tasmanian species belongs to a lineage with well developed dorsolateral plates. The stylus is hypertrophied but the problem of space is partly solved by the stylus being twice folded back on itself (Fig. 5A). The dorsal plate is also elongate and closely integrated with the stylus, bifurcating into two lobes just below the stylus tip. The ventral plate setae are greatly hypertrophied and differentiated into different forms (Fig. 5B). This species also has a short triangular sternum (though not unlike the female) and an elongate genital operculum (Figs 5J-K).

Thelbunus n.sp. has a less elaborate stylus and its sternum less modified and genital operculum less elongate (sternum illustrated in Fig. 6).

OTHER OPILIONES

Hypertrophy of the stylus has also been recorded in the neopilionid *Ballarra* spp (suborder Palpatores) from Australia (Hunt and Coken-

FIG. 2. Hypertrophied ♂ genitalia of *Chuniella* spp. A, B: *C. distincta*, A = lateral, B = ventral view of ventral and dorsolateral plates. C, D: *C. minuta*, lateral and ventral.

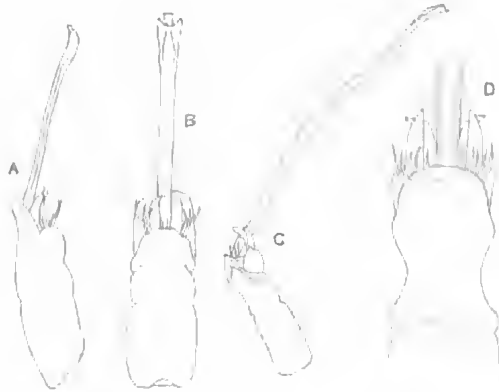


FIG. 3. Hypertrophied δ genitalia of South American Triaenonychidae. A, B: *Araucanobunus juberthiei*, lateral and ventral. C, D: New genus, new species (Maury, in prep.), lateral, ventral (part).

dolpher, 1991). Unlike the situation in *Cluniella* spp. and the South American species, the spermathecae are greatly elongate, opening into a short vagina but ending basally in the ovipositor. The long stylus is presumably inserted down the elongate spermatheca, not an elongate vagina as occurs in *Cluniella*.

Other taxa exhibit elongation of the truncus, e.g., many species of the triaenonychid genus *Lomanella* (Hunt and Hickman, 1993).

DISCUSSION

An elongate stylus is frequently, but not invariably, associated with an elongation of the genital operculum and a shortening and broadening of the sternum which together serve to elongate the cavity in which the penis lies (also, shortening of the truncus may compensate for the elongate stylus).

These changes in genitosternal architecture seem to have arisen independently in several distantly related genera. Within the one genus, both normal and hypertrophy-related genitosternal architecture can occur. For example, *Cluniella minuta* has evolved a moderately elongate stylus while retaining a 'normal' long, narrow sternum and rounded genital operculum. *C. distincta* has undergone much greater elongation of the stylus with consequent changes in the sternum and genital operculum.

It seems more probable that the situation in *C. minuta* is more 'primitive', while the syndrome of extreme characters in *C. distincta* represents a more derived condition. Thus, in the *Cluniella* lineage, space limitations of an elongate stylus

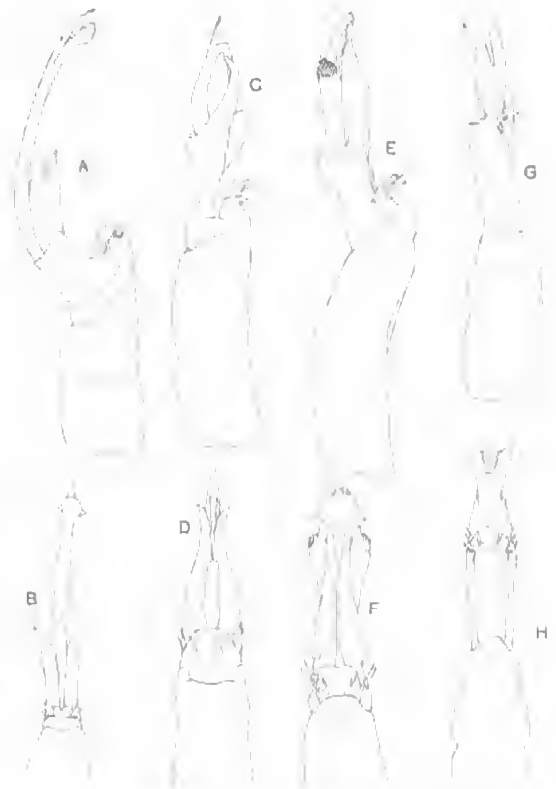


FIG. 4. Hypertrophied δ genitalia in Tasmanian Triaenonychidae. A, B: *Rhynchobunus arrogans*, lateral and ventral. C, D: *Tasmanobunus parvus*, lateral and ventral. E, F: *Tasmanonuncia* n.sp. (Hunt, in prep.), lateral and ventral. G, H: *Allobunus distinctus*, lateral and ventral.

seem initially accommodated by shortening of the truncus (*C. minuta* condition). Changes to the genital operculum and sternum evolved later.

Cluniella spp. and the two South American species described above show close correspondence in many features associated with stylus hypertrophy: great elongation of stylus, modification of sternum and genital operculum, shortening of truncus, and spermathecae situated basally in the ovipositor at the end of a very long vagina.

The question is whether these features indicate a close phylogenetic relationship or whether they are examples of convergence. The latter is supported because:

1. Modifications to genitosternal architecture appear to have arisen independently within the *Cluniella* lineage, evolving from the 'normal' condition as occurs in *C. minuta*.
2. Attachment of penis sheaths is basal in *Cluniella* and mesial in South American species.
3. The penes of the South American species

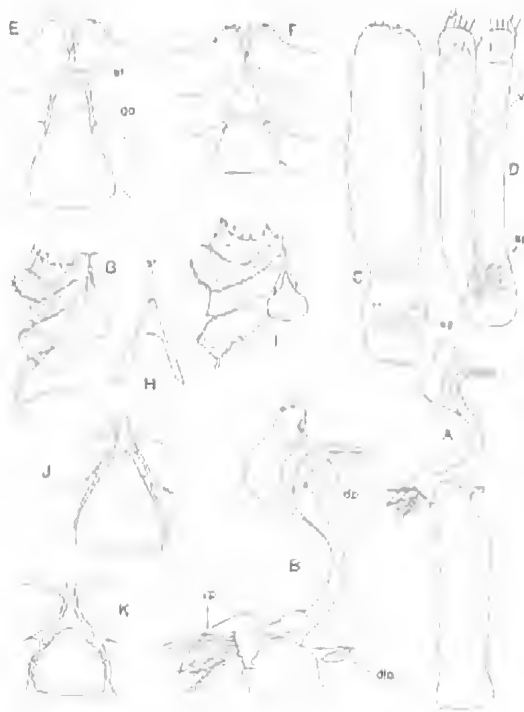


FIG. 5. Hypertrophy of genitalia in *Thelbunus mirabilis* and modified structures associated with genital hypertrophy in various Triaenonychidae. A, B: *T. mirabilis*, lateral and detail of lateral showing hypertrophy and modification of ventral plate setae. C, D: Ovipositor in *Cluniella distincta* and *Araucanobunus juberthiei* respectively showing basal seminal receptacles. E, F: Genitosternal region of *C. distincta*, ♂ and ♀ respectively. G, I: Genitosternal region of South American new genus, new species (Maury, in prep.), ♂ and ♀ respectively; H = shape of sternum in ♂ after genital operculum removed. J, K: genitosternal region of *T. mirabilis*, ♂ and ♀ respectively; go = genital operculum; sp = spermatheca; st = sternum; v = vagina (not delineated in *C. distincta*).

show closer affinity with the South American genus *Triaenonychoidea* (see Maury, 1987)) rather than with Australian genera.

4. Apart from the basal spermathecae and long vagina, the ovipositor of the South American species appears to be of the typical triaenonychid form. The ovipositor of both *Cluniella* spp. is highly derived in having a very membranous tip, in lacking well developed sensory lobes, and in carrying vestigial setae. In some specimens examined the membranous tip was inflated and had 'ballooned' out the genital orifice. This morphology suggests that the female may assist penetra-

tion by inflating the ovipositor so that it partly engulfs the stylus. Thus, assuming that the male *C. minuta* has not undergone a reversal in genitosternal architecture, the derived ovipositor seems to have evolved before shortening of the male sternum and elongation of the genital operculum.

Thus, the genomes of *Cluniella* and the two South American taxa have the capacity to allow quite remarkable convergence in a syndrome of characters. The overall effect appears the same, but the details differ.

Why have such vastly elongate styluses evolved, particularly to the extreme shown by *C. distincta*? Sexual selection by female choice is favoured by Eberhard (1985) as the most generally applicable explanation for 'extravagant' genitalia. Eberhard proposes that 'male genitalia function as 'internal courtship' devices to increase the likelihood that females will actually use a given male's sperm to fertilize her eggs rather than those of another male'. In the case of *Cluniella* and the South American species, it is postulated that males with the largest styluses have greater success than males with smaller styluses and hence contribute more of their genes to the next generation. The genitalia may stimulate the female prior to or during copulation and so activate the appropriate responses, or it might provide the right mechanical and sensory 'fit' during copulation. The basal spermathecae in the ovipositor of *Cluniella* spp. and the two South American species (and the long stylus matching the long spermathecae in *Ballarra* spp.) suggest that the correct mechanical fit may at least be part of the answer.

A search for congeners and an analysis of inter- and intraspecific variation, as well as behavioural studies, may yield further data to resolve these questions.

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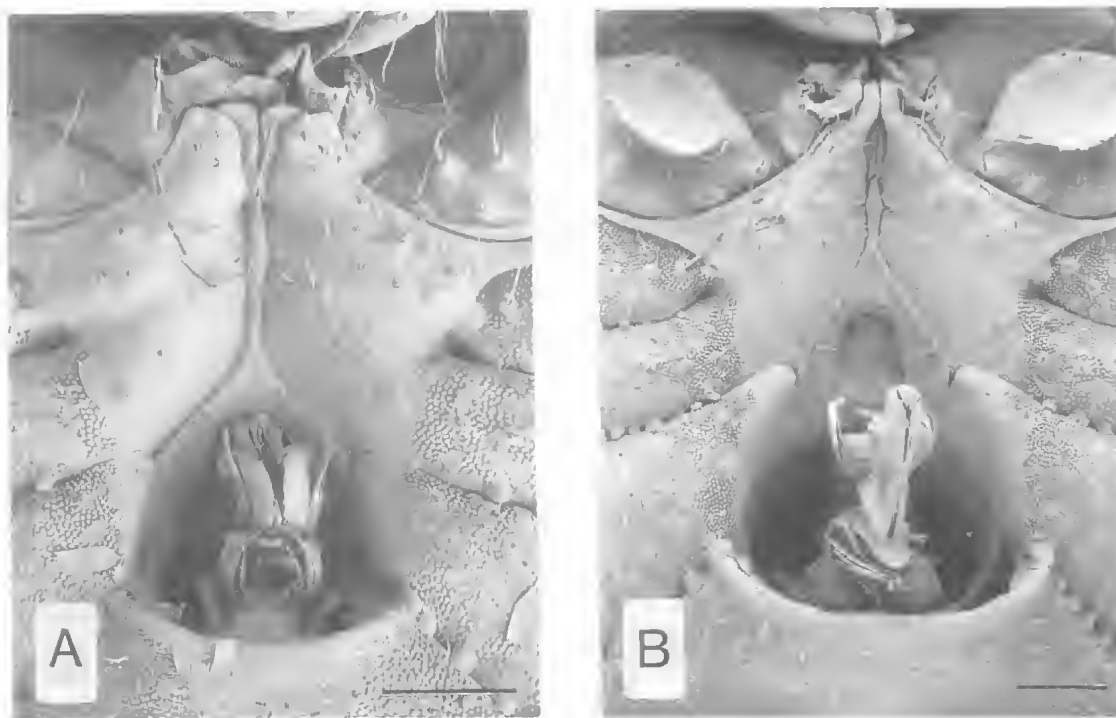


FIG. 6. Genitosternal region in *Thelbunus* spp. and variation in sternum; A = sp. nov.; B = *T. mirabilis*. Genital operculum lifted; note recess in sternum where folded stylus fits. Scale bars = 500 μ m.

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